THE Ds LOCUS. PART III. TRANSPOSITION OF THE Ds LOCUS

1. Introduction

Transposition of the Ds locus is a relatively frequent phenomenon. In the report on the origin and behavior of the c-ml locus, it was shown that c-ml arose from a normal C locus as the consequence of a transposition of a Ds locus from its standard location in chromosome 9 to a position close to or within the C locus. The presence of the transposed Ds locus did not produce any alteration in the appearance of the chromosome in the region where it had been inserted, nor did its presence cause any reduction in crossing-over between C and Sh. In this new location, Ds responded to Ac in exactly the same way that it responds to Ac when in its standard location. The relation of this response to the production of visible mutations of c-ml to C was discussed in the earlier report. The study of c-ml mutational phenomena suggested that the Ac-controlled mutable loci arise because of transpositions of the Ds locus. Since these transpositions are relatively frequent, it may readily be understood why so many new Ac-controlled mutable loci are arising in the Ds, Ac plants and why previously stable "wild-type" loci "suddenly" become unstable and mutable.

Because transpositions of Ds are related to the origin of mutable loci, it is of prime importance to determine the mechanism responsible for this transposition. How does it occur and why does it occur with such relatively high frequencies? An extensive analysis of one case of transposition of Ds has indicated the

probable mechanism that brings about this transposition. The analysis also suggests the reason why these transpositions are so frequent. This case of transposition of Ds will be considered in detail in this report.

2. The origin of transposed Ds, Case I

The first recognized case of transposition of Ds arose in the cross of a plant (4108C-1) having the constitution wd I Sh Bz Wx Ds in one normal chromosome 9 and Wd C sh bz wx ds in a normal homologous chromosome 9. This plant was heterozygous for Ac (Ac ac). The types of kernels resulting from the cross of this plant to a female plant carrying C sh bz wx ds ac are given in table 1. (The male parent plant (4108C-1) arose from an I - C bz, Sh - sh, Wx-wx kernel on an ear coming from the cross of a C sh bz wx ds ac female plant by an Ac ac male plant having two normal chromosomes 9 with Wd C Sh Bz Wx Ds and wd I Sh Bz Wx ds, respectively. The kernel from which plant 4108C-1 arose was selected because it had received an I Sh Bz Wx Ds chromosome. The Ds locus was introduced into this chromosome as a consequence of crossing-over in the heterozygous male parent.) As table 1 shows, with the exception of two aberrant kernels, the types of kernels and the ratios obtained are those expected on the basis of the above given constitution of this plant. When this plant was crossed to a c sh Bz wx ds ac female plant, the types of kernels appearing on the ear are those given in table 2. The ratios of the various types of kernels obtained in this cross likewise agree with the given genic constitution of the male parent plant (4108C-1; see supplement to table 2). In both crosses, the variegation in those kernels having both Ds and Ac is of the

Table 1

Types of kernels appearing on ear from cross of

C sh bz wx ds ac ♀ x $\frac{\text{I Sh Bz Wx Ds}}{\text{C sh bz wx ds}}$ Ac ac ♂

Plant 4108C-1

Kernel type	Number of kernels	
I-C bz, Sh*, Wx-wx	57	
I Sh Wx	59	
C sh bz wx	128	
I sh wx	5	
C Bz-C bz, Sh, Wx-wx	5	
C Sh Bz Wx	2	
I Sh wx	52	
C Bz-C bz, sh, Wx-wx	0	
C sh Bz Wx	1	
C sh bz, Wx-wx	22	
C sh bz Wx	31	
I-C Bz-C bz, Sh, Wx-wx	1	Origin of Plant 4306
I-C Bz, Sh wx	1	Not tested
Totals	364	

* The Sh-sh variegation will not be indicated in the table. It may be understood to be present.

Supplement to Table 1

Types of chromatids produced by plant 4108C-1 and appearance of kernel in table 1

	1	2	3	4	
	I	Sh	Bz	Wx	Ds
					Ac ac
	C	sh	bz	Wx	ds

			Appearance of kernel	
Non Cross-over chromatids	I Sh Bz bz Wx Ds	Ac	I-C bz, Sh-sh, Wx-wx	57
		ac	I Sh Wx	
	C sh bz wx ds	Ac and ac	C sh bz wx	
Region 1	I sh bz wx ds	Ac and ac	I sh wx	5
	C Sh Bz Wx Ds	Ac	C Bz-C bz, Sh-sh, Wx-wx	5
		ac	C Sh Bz Wx	2
Region 2	I Sh bz wx ds	Ac and ac	I Sh wx	
	C sh Bz Wx Ds	Ac	C Bz-C bz, sh, Wx-wx	0
		ac	C sh Bz Wx	1
Region 3	I Sh Bz wx ds	Ac and ac	I Sh wx	
	C sh bz Wx Ds	Ac	C sh bz Wx-wx	22
		ac	C sh bz Wx	31
Region 4	I Sh Bz Wx ds	Ac and ac	I Sh Wx	
	C sh bz wx Ds	Ac and ac	C sh bz wx	

Observed double cross-over, Regions 2 and 3 :-1 C sh Bz wx non-variegated

Odd classes = 2. See Table 1.

Table 2

Types of kernels appearing on ear from cross of

c sh Bz wx ds ac ♀ x $\frac{\text{I Sh Bz Wx Ds}}{\text{C sh bz wx ds}}$ Ac ac ♂

Plant 4108C-1

Kernel type	Number of kernels
I-C Bz, Sh*, Wx-wx	41
I Sh Wx	68
C sh wx	86
I sh wx	4
C-c, Sh, Wx-wx	3
C Sh Wx	1
I Sh wx	48
C-c, sh, Wx-wx	14
C sh Wx	24
I sh Wx	1
Totals	290

162 I : 128 C
152 Wx : 138 wx

* The Sh-sh variegation will not be indicated in the table but may be understood to be present.

Supplement to Table 2

Chromatids produced by plant 4108C-1 and appearance of kernels:

Cross-over regions tested:

I	Sh		Wx	Ds
C	sh		wx	ds
	1	2		3

Cross-over region	Constitutions of ♂ gametes		Resulting kernel type	Critical kernels
Non-crossovers	I Sh Wx Ds	Ac	I-c Sh Wx-wx	41
		ac	I Sh Wx	
	C sh wx ds	Ac and ac	C sh wx	
Region 1	I sh wx	Ac and ac	I sh wx	4
	C Sh Wx Ds	Ac	C-c Sh Wx-wx	3
		ac	C Sh Wx	1
Region 2	I Sh wx ds	Ac and ac	I Sh wx	48
	C sh Wx Ds	Ac	C-c sh Wx-wx	14
		ac	C sh Wx	24
Region 3	I Sh Wx ds	Ac and ac	I Sh Wx	
	C sh wx Ds	Ac	C-c sh wx	0
		ac	C sh wx	

Regions 1 and 2: 1 I sh Wx (Ds ac).

type expected when a Ds locus is at its standard position in the I Sh Bz Wx chromosome. The Ds mutations gave rise to C sh bz wx sectors (table 1) or c sh wx sectors (table 2). Also, the position of this Ds locus is obvious from the types and frequencies of recovered cross-over chromatids shown in tables 1 and 2. There can be no doubt that in plant 4108C-1, Ds was located to the right of Wx,--at its standard location in the wd I Sh Bz Wx chromosome.

One of the two exceptional kernels listed in table 1 showed a type of variegation that would not arise from an I Sh Bz Wx Ds order of genes. In this kernel, many chromosome breaks of the Ds mutational type had occurred, but the position of the breaks was just to the right of the I locus instead of to the right of the Wx locus. These breaks gave rise to cells in which the I locus was eliminated but the Sh Bz and Wx loci were retained. Following such a Ds mutation, a dicentric chromatid was formed that had Sh Bz and Wx in the short arms of the two terminally fused chromatids (the dicentric chromatid). Continued breakage-fusion-bridge cycles resulted in successive deletions of these loci in some of the descendent cells. Consequently, within the C Bz Wx sector sub-sectors of bz and wx were present. Another type of variegation was also present but the description of the variegation types will be postponed until later when correlations of the genic organization of this chromosome with the variegation patterns can logically be derived.

The aberrant kernel was planted in the greenhouse in the winter of 1947-48. No cytological examination was made of the plant arising from this kernel for fear of injury. Because the plant was very early in maturing and because no other plants were available for crossing, only a self-pollination of this plant was possible. The

types of kernels appearing on this self-pollinated ear are given in table 3. The chromosomal and genic constitution of the aberrant chromosome 9 carrying I Sh Bz Wx in this plant has been determined from an analysis of the plants arising from the kernels on this self-pollinated ear. This analysis makes the types of kernels that appeared on the ear readily interpretable. Because the kernels are quite different from those arising in previous studies, a supplementary analysis giving the chromatids that could be produced during meiosis in this plant and the types of gametes that will result accompanies table 3. This plant had a normal chromosome 9 carrying C ds sh bz wx ds and a Duplication chromosome 9 with wd ~~and~~ I, ~~and~~ Sh Bz Wx (was carried) in each of the two duplicated segments (see diagram, table 3 supplement). Synapsis between the two chromosomes 9 usually occurs as given in the diagram and the crossover percentages between the marked loci are not reduced, as the genetic analysis of the F_2 plants that were heterozygous for this duplication will show. The "ds" designation is meaningless with respect to the presence of any true allelic loci. It has been inserted to make the constitutions easier to read at a glance. Because of the many possible classes of crossover chromatids that could arise in this plant, only the single crossovers between the two chromosomes 9 following synapsis of the distal duplicated segment in the Duplication chromosome 9 with its homologous segment in the normal chromosome 9 are given in the supplement to table 3. Double crossovers in the region between C and wx are relatively rare and will be neglected at this point in the discussion. The single crossovers, however, are frequent and are most important in interpreting the constitutions of the observed types of kernels. Although it was realized from the types of kernels on the self-pollinated ear that

Table 3

Types of kernels appearing on self-pollination of Plant 4306

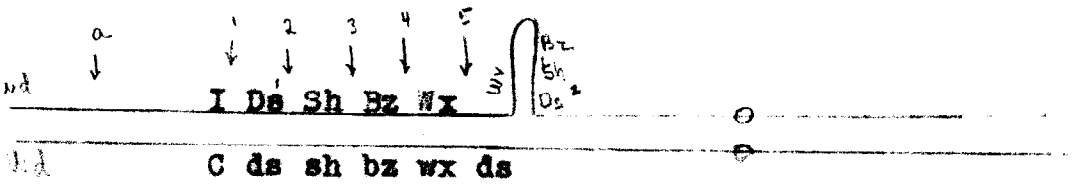
Constitution: wd I Ds' Sh Bz Wx Wx Bz Sh Ds²

Wx C ds sh bz wx ds — — — — Ac ac

I kernels		C kernels	
I Sh Wx	81	C Sh Bz Wx	4
I Sh Wx-wx	6	C Bz-C bz, Sh-sh, Wx-wx	3
I-C Bz-C bz, Sh-sh, Wx-wx	73	C sh bz wx	89
I-C Bz, Sh Wx	1		
I Sh wx	4	Total : 274	
I-C Bz-C bz, Sh-sh, wx	10	178 I : 96 C	
I sh wx	2	168 Wx : 106 wx	
I bz-C bz, sh wx	1		

Supplement to Table 3

Types of chromatids produced by plant 4306. Non-crossover and single cross-over chromatids resulting from the usual type of synapsis. The expected appearance of the kernel if combined with a C sh bz wx ds chromosome in Ac ac ac or ac ac ac constitution



Chromatids			Appearance of kernel
Non-crossovers	I Ds' Sh Bz Wx Wx Bz Sh Ds' Duplication	Ac	I-C Bz-C bz, Sh, Wx-wx
		ac	I Sh Wx
	C ds sh bz wx ds normal	Ac and ac	C sh bz wx
	I ds sh bz wx ds normal	Ac and ac	I sh wx
Region 1	C Ds' Sh Bz Wx Wx Bz Sh Ds' Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Region 2	I Ds' sh bz wx ds normal	Ac	I bz-C bz, sh wx
		ac	I sh wx
	C ds Sh Bz Wx Wx Bz Sh Ds' Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx

Supplement to Table 3 continued

Region 3	I Ds' Sh bz wx ds normal	Ac	I bz-C bz, Sh wx
		ac	I Sh wx
	C ds sh Bz Wx Wx Bz Sh Ds' Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Region 4	I Ds' Sh Bz wx ds normal	Ac	I-C Bz-C bz, Sh wx
		ac	I Sh wx
	C ds sh bz Wx Wx Bz Sh Ds' Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Region 5	I Ds' Sh Bz Wx ds normal	Ac	I-C Bz-C bz, Sh, Wx-wx
		ac	I Sh Wx
	C ds sh bz wx Wx Bz Sh Ds' Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Region a Not considered in table	Wd I Ds' Sh Bz Wx Wx Bz Sh Ds' Duplication	Ac	I-C Bz-C bz, Sh, Wx-wx
		ac	I Sh Wx
	wd C ds sh bz wx ds normal	Ac and ac	C sh bz wx

(1) a Ds locus had been transposed just to the right of the I locus and that (2) some chromosomal aberration involving the region to the right of the I locus had likewise occurred, the exact nature of the aberration was not clearly understood from the analysis of this ear alone.

To obtain exact information on the aberration that occurred and its possible relation to a transposition of Ds, some of the kernels in the various classes represented in table 3 were planted in the summer of 1948 under culture number 4628. With respect to Wd or wd and Bz or bz, the types of plants arising from these various classes of kernels are given in table 4.

3. Cytological examination of plants in culture 4628.

Cytological examination was made of a number of plants in the various sub-classes of culture 4628. The sporocytes in some of these plants gave very poor figures. Those in which the constitution of chromosome 9 was clear and readily analyzable are summarized in table 5. In sub-cultures D and E, the majority of plants probably had the same genic as well as chromosomal constitution as the mother plant. All the examined plants had one normal chromosome 9 and a chromosome 9 with a duplication of a mid-segment of the short arm. This duplicated segment was inserted into the short arm. Homologous synaptic association of the short arm of the normal chromosome 9 with the short arm of the Duplication chromosome 9 usually occurred along the distal two-thirds of the arm. A loop configuration in the Duplication chromosomes 9 was present. Its position varied in the different sporocytes but it was usually close to or within the deep-staining region adjacent to the centromere. None of this proximal

Table 4

Appearance of plants in culture 4628 obtained from selected ~~groups of~~ kernels on self-pollinated ear of plant 4306 (table 3)

Sub-culture designations	Appearance of kernel in each sub-culture from which plants arose	Number of kernels planted		Appearance of plants arising from kernels
A	I-C Bz, Sh Wx	1	0	No shoot developed; only roots
B	I Sh Wx-wx	2	2	white seedlings (wd/wd)
C	I Sh Wx	20	17	Wd, Bz : 1 white : 2 no germination
D	I-C Bz-C bz, Sh-sh, Wx wx (Many C bz wx areas)	15	15	Wd, Bz
E	I-C Bz-C Bz, Sh-sh, Wx-wx (Few C bz wx areas)	10	8	Wd, Bz : 1 white : 1 no germination
F	I Sh wx	2	2	Wd, Bz
G	I-C Bz-C bz, Sh-sh, wx (Many C bz areas)	3	3	Wd, Bz
H	I-C Bz, Sh-sh, wx (Few C bz areas)	2	2	Wd, Bz
I	I sh wx	2	2	Wd, bz
J	I bz-C bz, sh wx	1	1	Wd; died in seedling stage
K	C Sh Bz Wx	2	2	Wd, Bz
L	C Bz-C bz, Sh-sh, Wx-wx	2	2	Wd, Bz
M	C sh bz wx	20	6	Wd, bz

Table 5

Constitutions of chromosomes 9 in plants of culture 4628 based upon examination of sporocytes at pachytene.

Plant Number	Constitution of chromosomes 9 in examined plant	Constitution of plant from pollen examination
4628C- 9	2 Duplications chromosomes 9	Wx Wx
4628C-17	1 Duplication chromosome 9 1 Normal " "	Wx wx
4628D-10	1 Duplication " " 1 Normal " "	Wx wx
4628D-11	1 Duplication " " 1 Normal " "	Wx wx
4628D-12	1 Duplication 1 Normal	Wx wx
4628E- 8	1 Duplication 1 Normal	Wx wx
4628F- 1	2 Normal	wx wx
4628F- 2	2 Normal	wx wx
4628G- 1	2 Normal	wx wx
4628G- 2	2 Normal	wx wx
4628H- 1	2 Normal	wx wx
4628H- 2	2 Normal	wx wx
4628L- 1	1 Duplication 1 Normal	Wx wx

deep-staining region, however, was included in the duplicated segment.

Plant 4628C-9 was homozygous for the chromosome 9 with the duplication. By comparative measurements of the short and long arms of chromosome 9 in this plant and from the appearance of the chromomeres within this arm, it was apparent that the duplication was composed of a segment approximately equivalent in length to a third of the normal short arm. It was composed only of the smaller chromomeres characteristic of the distal two-thirds of the normal short arm. It was concluded (1) from the chromomere constitution in the plant homozygous for this duplication, (2) from the synaptic phenomena in the heterozygous plants and (3) from the genic and chromosomal constitutions of the F_2 population that the duplicated segment was composed of a section of the middle of the short arm of chromosome 9 and of a length approximately one-third of this arm. This segment had been inserted into a normal short arm. This may be diagrammed, without reference to order of genes, as follows:

Normal chromosome 9 short arm:

Duplication chromosome 9 short arm:

Plant 4628L-1, arising from a kernel having a cross-over chromatid, was heterozygous for the Duplication chromosome 9. Synaptic behavior between the normal and the Duplication chromosome 9 was similar to that described for the heterozygous plants in sub-cultures D and E. The plants in sub-cultures F, G and H, on

the other hand, had two morphologically normal chromosomes 9. No abnormalities of any kind could be seen in the chromosomes 9 of these plants. In all of these plants, however, the I, Ds, Sh and Bz loci in the normal chromosome 9 had originally been located in the Duplication chromosome 9 of the mother plant.

A genetic analysis of the plants of culture 4628 has made it possible to state (1) the genic composition of the two identical segments in the Duplication chromosome 9, (2) the order of the genes in each segment and (3) the probable event that occurred in a cell of plant 4108C-1 which produced the duplication and the transposition of a Ds locus from its standard position to a position immediately to the right of the I locus. The purpose of the following description is to give the evidence that allows these conclusions to be drawn.

4. The genetic analysis of the plants in culture 4628. (a). Sub-culture C.

Pollen examinations were made of a number of plants of culture 4628 (table 6). This was particularly important in sub-culture C in order to select those plants that could be expected to be homozygous for the Duplication chromosome 9. These plants should be Wx Wx. Only 3 Wx Wx plants were present in this sub-culture. Because plant C-9, a Wx Wx plant, had also been examined cytologically, it was selected for tests to determine the types of variegation patterns that the Ds loci in the Duplication chromosomes 9 would produce. This plant was crossed to the following female plants:

Table 6

Wx and wx constitutions in plants of culture 4628 based on pollen examination

Sub-culture	Wx Wx*	Wx wx	wx wx	Appearance of kernels from which plant arose
C	3	14	0	I Sh Wx
D	0	3	0	I - C Bz - C bz, Sh-sh, Wx-wx
E	0	1	0	I - C Bz - C bz, Sh-sh, Wx-wx (few C bz areas)
F	0	0	2	I Sh wx
G	0	0	3	I - C Bz - C bz, Sh-sh, -wx
H	0	0	2	I - C Bz, Sh-sh, wx (few C bz areas)
I	0	0	2	I sh wx
K	0	2	0	C Sh Bz Wx
L	0	2	0	C Bz - C bz, Sh-sh, Wx-wx

* All 3 plants had a few, small, partially filled wx staining pollen grains. This is to be expected from Ds^2 mutations (see Annual Report, 1948).

(1) C sh bz wx ds, ac ac

(2) C sh bz wx ds, Ac ac

(3) c sh Bz wx ds, ac ac

(4) C Sh Bz wx Ds / C Sh Bz wx Ds, Ac Ac

(5) C Sh Bz wx Ds/ C Sh Bz wx Ds, ac ac

When crossed to C sh bz wx ds ac female plants, two types of kernels appeared on the ears in equal ratios. One was I Sh Wx and non-variegated. The other type of kernel was variegated (table 7-a). All these variegated kernels had sectors that had lost the I locus. Many of the sectors were C Bz Wx in phenotype but within the sector variagation for C bz was present. These C bz areas were all wx. Within the C Bz sectors there were often large wx areas that were definitely Bz and not bz. This is important, as will be indicated later. There were also some C bz wx sectors, not within or associated with the C Bz sectors. It was evident that two types of events were occurring in these kernels. Both involved loss of the I locus but one gave the C Bz Wx sectors with C bz wx and Bz wx areas within them and one gave C bz wx sectors directly. Further analysis has made it clear that these two separate types of variegation are associated with the presence of two Ds loci in the Duplication chromosome 9, one (Ds^1) located just to the right of the I locus and one (Ds^2) located to the right of the proximal duplicated segment. A Ds^2 mutation accounts for the appearance of the independent C bz wx sectors; a Ds^1 mutation gives rise to the C Bz Wx sectors with a secondary type of variegation within them, as described above: (produced by breakage - fusion - bridge cycles following the formation of the dicentric chromatid from a Ds' mutation).

Table 7-a

C sh bz wx ds ac ♀ x $\frac{\text{I Ds}^1 \text{ Sh Bz Wx Wx Bz Sh Ds}^2}{\text{I Ds}^1 \text{ Sh Bz Wx Wx Bz Sh Ds}^2}$ Ac ac ♂

Plant 4628C-9

Cross	Kernel types	
	I Sh Wx	I-C Bz-C bz; Sh-sh, Wx-wx*
4361-5 x 4628C-9	222	212
4363-10 x " "	18	16
4362C-6 x " "	273	236
Totals	513	464

* See text for accurate description of variegation.

Table 7-b

c sh 9z wx ds ac ♀ x 4628C-9 ○

Cross	Kernel types: Colorless Sh Wx	Kernel types: Colorless Sh-sh Wx-wx
4347-19 x 4628C-9	180	189

Table 7-c

C sh bz wx ds, Ac ac 9 x 4628C-9

Cross	I Sh Wx* not obviously variegated (Ac Ac Ac and ac ac ac)	I-C Bz-C bz, Wx-wx Speckled (Ac Ac ac)	I-C Bz-C bz, Wx-wx Ac ac ac type	Odds
4462C-11 x 4628C-9	190	121	140	
4462C-1 x " "	171	115	110	1 C Sh Bz Wx non-variegated
Totals	361	236	250	1

* Some of the kernels in this column have a few small C areas or a few specks of C.

Table 7-d

C Sh Bz wx Ds / C Sh Bz wx Ds, Ac Ac ♀ x 4628C-9 ♂

Cross	I Wx not obviously variegated (Ac Ac Ac)	I-C, Wx-wx Ac Ac ac type	I-C, Wx-wx Ac ac ac * type
4380B-6 x 4628C-9	25	36	1

* See report on Ac locus for explanation of this type of kernel variegated

The evidence obtained from this cross alone is not sufficient to establish the genic constitutions of the chromosomes 9 in this plant (4628C-9) as given in table 7-a. The analysis of the other plants in culture 4628 allows the genic constitutions of the chromosomes 9 in this plant to be designated with a high degree of certainty. The constitution of the Duplication chromosomes 9 are, then: I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2.

That no C locus was present in the duplication chromosome 9 was indicated from the cross of 4628C-9 to c sh Bz wx ds ac female plants (table 7-b). All of the kernels resulting from this cross were colorless. No colored spots or areas were seen in any of them. Half of them, however, were Wx - wx variegated, as expected. If a C locus had been present to the right of Ds^1, then its presence should have been detected in the Wx - wx variegated kernels on this ear. It seems reasonable to conclude, therefore, that no C locus was present in the Duplication chromosome 9. That none should be present will be indicated when the projected event that gave rise to the duplication is discussed.

Plant 4628C-9 was crossed to a C sh bz wx ds, Ac ac female plant, table 7-c. If plant 4628C-9 were Ac ac in constitution, as the evidence in tables 7-a and 7-b indicate, the endosperm constitutions of the kernels represented in table 7-c should be 1 Ac Ac Ac : I Ac Ac ac : 1 Ac ac ac : 1 ac ac ac. Responses of the Ds loci to Ac dosage would determine the classes of kernels appearing on this ear. The ratios of classes, with respect to variegation pattern, in table 7-c, are those that could be anticipated. The observations suggest that some of the Ac Ac Ac constitutions allow a very light speckled pattern of variegation to appear--a few very late Ds muta-

tions were occurring in some of these kernels. Table 7-d gives the types of kernels obtained from the cross of 4628C-9 to a C Sh Bz wx Ds C Sh Bz wx Ds, Ac Ac (allelic positions) female plant. Again, the classes of kernels appearing on the ear following this cross are in agreement with the projected constitution of the male parent.

(b). Sub-culture D

The tested plants in sub-culture D were all heterozygous for the Duplication chromosome 9. The selection of this class of kernels from the self-pollinated ear of plant 4306, would suggest that they might have similar chromosome and genic constitutions as the mother plant. Two of these plants were crossed to C sh bz wx ds ac female plants. The results of these crosses are given in table 8. Because of the many classes of kernels that could appear following this cross, a supplement to table 8 has been included to show the types of chromatids that these plants could produce, if they had the given chromosome 9 constitutions. The types of chromatids are the same as those that have been considered for the parent plant. (Supplement to table 3). In these crosses, however, a direct test for the presence of these various types of non-crossover and crossover chromatids is available. It may be seen from the supplement to table 8 that crossing over would produce morphologically normal chromosomes 9 having a transposed Ds locus. The constitutions of these chromosomes, in the single cross-over classes, would be: I Ds' sh bz wx, I Ds' Sh bz wx and I Ds' Sh Bz wx. The variegation pattern that each of these chromosomes would produce in the cross to C sh bz wx ds is apparent. They appear in table 8 under the designated headings I bz-C bz, sh, wx, I bz-C bz, Sh-sh, wx and I-C Bz-C bz, Sh-sh, wx, respectively. If plants

Table 8

C sh bz wx ds ac ♀ x $\frac{\text{I Ds}^1 \text{ Sh Bz Wx Wx Bz Sh Ds}^2}{\text{C ds sh bz wx ds}}$ Ac ac ♂

Kernel type	Cross 4363-6 x 4628D-10	4363-11 x 4628D-10	4363-17 x 4628D-11	4462C-8 x 4628D-11	Totals
I Sh Wx	38	55	37	70	200
I-C Bz-C bz, Sh*, Wx-wx	16	27	40	59	142
I Sh wx	22	29	13	30	94
I-C Bz-C bz, Sh, wx	8	16	19	33	76
I bz-C bz, Sh, wx	1	1	1	0	3
I sh wx	3	5	2	8	18
I bz-C bz, sh wx	1	3	2	6	12
C Sh Bz Wx	20	16	16	27	79
C Bz-C bz, Sh, Wx-wx	10	7	7	19	43
C Sh Bz wx	0	0	1	2	3
C sh bz wx	67	115	108	210	500
			Total kernels		1170

* The Sh-sh variegation will not be indicated in the table but may be understood to be present.

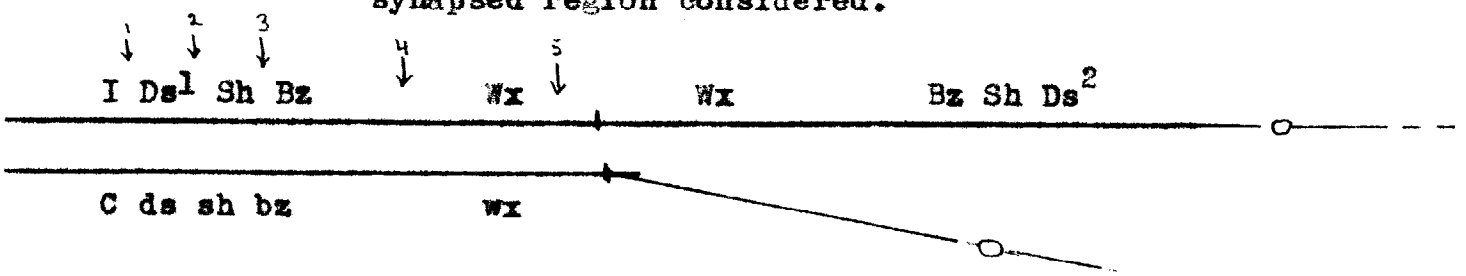
545 I : 625 C

385 wx : 785 wx

4628D

Supplement to Table 8

Types of chromatids produced by ♂ plants in table 8. Only single cross-overs in designated synapsed region considered.



			Appearance of kernel in Table 8
Non-crossovers	I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2	Ac	I-C Bz-C bz, Sh, Wx-wx
	Duplication	ac	I Sh Wx
	C ds sh bz wx ds normal	Ac and ac	C sh bz wx
Cross-overs Region 1	I ds sh bz wx ds normal	Ac and ac	I sh wx
	C Ds^1 Sh Bz Wx Wx Bz Sh Ds^2	Ac	C Bz-C bz, Sh, Wx-wx
	Duplication	ac	C Sh Bz Wx
Crossovers Region 2	I Ds^1 sh bz wx ds	Ac	I bz-C bz, sh wx
	Normal	ac	I sh wx
	C ds Sh Bz Wx Wx Bz Sh Ds^2	Ac	C Bz-C bz, Sh, Wx-wx
	Duplication	ac	C Sh Bz Wx

Supplement to Table 8 continued

Crossovers Region 3	I Ds^1 Sh bz wx ds / Normal	Ac	I bz-C bz, Sh, wx
		ac	I Sh wx
	C ds sh Bz Wx Wx Bz Sh Ds^2 / Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Crossovers Region 4	I Ds^1 Sh Bz wx ds / Normal	Ac	I-C Bz-C bz, Sh, wx
		ac	I Sh wx
	C ds sh bz Wx Wx Bz Sh Ds^2 / Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Crossovers Region 5	I Ds^1 Sh Bz Wx ds / Normal	Ac	I-C Bz-C bz, Sh, Wx-wx
		ac	I Sh Bz Wx
	C ds sh bz wx Wx Bz Sh Ds^2 / Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx